THE ANATOMY OF CALIFORNIAN HALIOTIDÆ.[1]

BY CLAYTON F. PALMER.

The past few years have witnessed great additions to our knowledge of the anatomy of mollusks, and in this phylum probably no group has received more attention than the prosobranchs. And it is equally true that while the bibliography relating to this last named division has assumed large proportions the results are often of a conflicting nature. Even the comparatively limited family of the Haliotidæ have received their share of consideration, and unfortunately a proportionate amount of confusion as well. It is thus apparent that the anatomy of *Haliotis* merits more study, especially on account of the position this mollusk occupies among archaic forms. Something over a year ago, while studying in the zoology department of Stanford University, Dr. Harold Heath suggested to me that the anatomy of *Haliotis* deserved further investigation. The western coast of North America is the habitat of several species of this mollusk, and two of these are readily procurable from the university. Therefore material was never lacking, and as it was of relatively giant size the following results are believed to be correct.

The material consisted of specimens of *Haliotis rufescens* Swn. and *H. cracherodii* Leach, the red and black abalone respectively. These were taken of various sizes and were examined both by gross dissection and in section. So far as I know, no anatomical details have ever been published concerning any species of *Haliotis* found in this part of the world. Hence the following may serve to corroborate, to some extent, certain facts relating to the genus, and to correct certain misstatements as well.

Upon opening the mantle cavity of *Haliotis*, one first sees the two well developed ctenidia of the distinct bilamellate type, the left being somewhat the larger. Near their bases and against the ventral wall of the rectum may be seen the papilla-like openings of the right and left ureters (text fig. A, *RU*, *LU*); the right aperture generally has the

[1] The present paper was completed over four years ago, and was intended to form a division of a more extended work relating to the anatomy of various mollusks from the western coast of the United States. Owing to other duties it is impossible to carry out the proposed plan, at least within the near future, and the results in their original form are herewith presented.

more tumid lips of the two. The left duct leads directly into the main cavity of the excretory organ, while the one of the other side opens into a kind of vestibule, which in turn communicates with the main body of the organ.

The *left kidney* in *Haliotis* (fig. 1, Pl. XXX, *LK*) has become greatly reduced and highly modified; it is now known generally as the papillary sac, a term applied to homologous organs in other members of the group. It lies against the left side of the rectum (*R*), and extends backward and to a certain extent over the anterior and left surface of the pericardial wall (*P*). With the exception of its right or inner side, where it is contiguous with the rectum, its walls are produced into well developed papillæ.

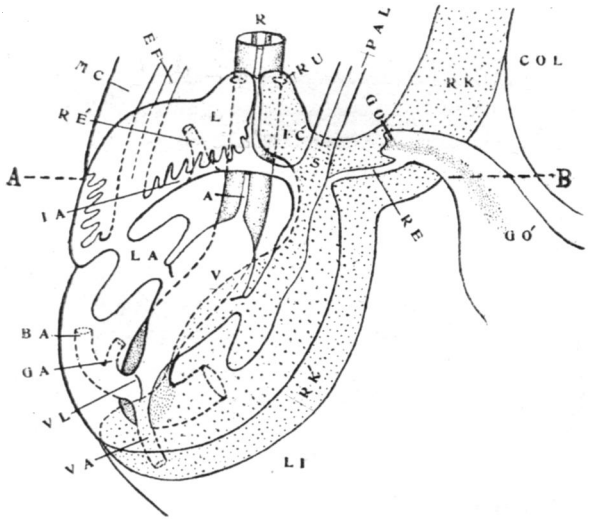

Fig. A.—Diagram showing relations of nephridia, pericardium, gonoduct, etc. For lettering see explanation of plate.

Just what functions are sustained by this organ is not clear, though several theories have been advanced. Pelseneer ('96) believes it is phagocytic in character. Its walls and papillæ are richly supplied with the purest blood; the organ seems to be the principal excuse for the existence of the peculiar inter-auricular sinus (fig. A, *IA*) described by other writers for this genus. This blood sinus connects the right and left auricles, coursing along the outer edge of the wall separating the pericardium and left kidney. In sections a connection may be traced between the wall of the papillary sac and the basibranchial sinus. Its

blood supply is similar therefore to that in European species of *Haliotis*, as described by Perrier ('89), Wegmann '(84) and other workers. Whatever function is served by the papillæ, it is very evident, judging from their appearance, that they are actively secretory by nature.

The *right kidney* (fig. A, *RK*, *RK'*) is the principal excretory organ in *Haliotis*. It is well developed and occupies, in the species under discussion, a position very similar to that described for the European species, *H. tuberculata* and *H. glabra* (Haller). From the small chamber (*IC'*) immediately behind the lobe (*RU*), serving as a mouth to the ureter, there is a species of vestibule opening posteriorly into larger cavities at the right (*RK*) and left (*RK'*). The junction of these is under the forward inner corner of the pericardium (*P*), the vestibule (*IC'*) corresponding in position to the papillary sac. The last named organ and the vestibule of the right kidney are separated by the rectum, which is supported between them by a thin dorsal and ventral partition, shown to some extent in fig. 3, Pl. XXX, although this section is too far posterior to indicate clearly their true relations.

Bouvier ('88) recorded an inter-renal communication in *Ampullaria*, but this is emphatically denied by Pelseneer ('96). Haller has reported such a state of affairs in *Haliotis "glabra"* and *Trochus "gibberosus,"* but very little acceptance has been accorded to the statement. Communication may possibly exist in certain mollusca, but it is doubtful if such a connection is present in the genus *Haliotis*. By referring to figs. 1, 3, 5 it will be seen that, in addition to the close contact of the two nephridia as just explained, they are in close proximity at the bottom of the chamber (*IC*). However, a careful examination of several series of sections through these regions gives no hint of any definite connection.

From its junction with the vestibule the cavity of the posterior part of the kidney (*RK'*) extends beneath the pericardium and around its inner and posterior surface. The lumen of the anterior portion (*RK*) is directed forward toward the columellar muscle. Near the latter it enlarges considerably in a dorso-ventral direction, and becomes in shape and size like an almond seed in specimens of average size. The outlines of the walls of the kidney itself correspond closely with the cavities just described, and accordingly are similar in all essential regards to the species described by Wegmann ('84), Totzaur ('02) and others.

The tissue of the right kidney is nowhere very thick; it is disposed more as an intervisceral packing material. The division (*RK'*) in the region of the pericardial cavity is a curved mass of spongy tissue, lying under and about the inner side of the pericardium and ending

immediately behind its postero-lateral corner. The intestinal lobe (*RK*) is somewhat strap-shaped and extends well forward toward the head. In color the right kidney is of a grayish brown tint, varying to a buff shade. Histologically the tissue consists of minute pouches, or acini, which open into small channels, these into larger ones, and so on to the main ducts. The cells are of the usual cubical form, and are crowded with pigmented waste products of granular appearance. I have seen nothing in my material that seems to warrant any further discussion of the tissue, which has been well described by others.

The *reproductive system* in *Haliotis* is interesting, among other things, because of the lateness of its development, and the rapidity of the same when once begun. Careful microscopical examination of small specimens reveals at best only the slightest development or not even a trace of a germinal epithelium. Even in specimens 3 cm. long the latter is demonstrated with difficulty. In average-sized individuals, and larger, the gonad is well developed, especially at the height of the breeding season, which occurs early in the year. The testis is of a cream color, the ovary a slaty green. There is practically no difference in size between the glands of the two sexes, very nearly the entire surface of the main visceral mass being covered by the organ.

In small specimens of *H. cracherodii*, of about 2 cm. in length, the whole of the visceral mass to the right of the pericardium, except one small area (a portion of the stomach), is of a brownish color. This is due to the extensive liver, which forms the horn-shaped portion of the visceral mass, extending along the right posterior curve of the columellar muscle. At the left of the cæcum the stomach is in contact with the body wall, and projecting through the liver forms the i regular whitish area noted above. Examined externally specimens fully 5 cm. in length show no changes from the condition just described. From this time forward, however, the development of sexual products commences to manifest itself. The first outward indication is a grayish tinge at the tip of the horn (of the visceral mass), which gradually extends itself over the remainder of the liver. Individuals 6, or at most 7, cm. in length possess a grayish coating entirely investing the horn. This thickens, and in specimens 8 cm. long there is a well established gonad extending to some extent over the main visceral mass. As may be supposed, the thickest part is at the tip of the horn, where it measures about 3 mm. in depth. The males and females of this size exhibit practically no difference in gonad coloration.

Sections through the gonad of males and females between 7 and 8 cm. long revealed sperms or ova that while immature are in well

advanced stages of development. The ova were of oval form, and the heads of the sperms were bacillus-shaped. Even under very high powers no filaments could be detected, though they may probably have been destroyed by reagents. The material, it should be added, was collected early in October, while the breeding season does not begin until some time in January or February. From the above it is evident that *H. cracherodii* does not commence to breed until it is more then 9 cm. in length, and it is certain that sexual activity begins at a somewhat earlier period with the males than the females.

In large specimens the gonad may attain as much as half an inch in thickness along the posterior border of the columellar muscle. And the cavity, only potentially present in early stages, becomes now very clearly defined and of considerable size. Tracing it posteriorly and then to the left one may discover the funnel-shaped gonoduct (*GO'*, figs. 2, 3, 4, 5, text fig. A). It bends somewhat to the left and narrows to a flattened tube from 3 to 6 mm. in diameter. This opens into the cavity of the kidney, at the left border of the gonad, and the mouth is provided with a flexible valve-like flap, which may serve to prevent the entrance of any substances from the kidney. I have found ripe eggs and sperms in the gonoducts of specimens taken the last of December. Perrier ('89) states that the gonoduct of *Haliotis* is closed except at the breeding season, but this is certainly not the case in the two species studied by me. In all stages the duct has been open and there was a free passage from the gonad to the kidney. There was no organic obstruction even in specimens 2 cm. long. Fleure ('02) found ova in the pericardial cavity of *H. tuberculata*, but this is probably an accidental occurrence, since in the western species the sex products pass from the kidney directly to the exterior.

The *renopericardial canals* of prosobranchs have of late been the subject of much controversy, and at the present time the results of various authors are decidedly conflicting. Working upon the European species Wegmann ('84), Perrier ('89) and Erlanger ('92), besides other investigators, found a left renopericardial canal only. Fleure ('02) examined the same species very carefully, but curiously could find no left canal, though he did demonstrate the existence of a right canal. About the same time Totzaur ('02) found both canals, but neither of these investigators has given us any figures nor a detailed account of these much discussed organs. Some time previous to the reports of the above named authors, Haller stated that he had found both canals in *H. glabra*, and was thus, so far as I am aware, the first to report such a state of affairs for any species of *Haliotidæ*.

Haliotis undoubtedly possesses two renopericardial canals. I have been able to demonstrate their presence, in the two species under discussion in this paper, both macroscopically and microscopically. They may be seen readily in material from upwards of 0.5 cm. in length (the smallest specimens I had) to that over 13 cm. long.

For a study of these canals it will be well to commence with a consideration of sections through specimens about 1.5 cm. long. The first five figures should give one a fairly clear idea of the relations of the renopericardial canals, pericardium, kidneys and gonoduct.[2] Neither of the canals is very long, and both may be regarded as funnel-like outgrowths of the pericardium. The left canal (*RE*) is, however, much the wider, and can be followed far more readily in material properly prepared.

The left renopericardial canal originates as a wide tube opening into the pericardial cavity somewhat ventral to the point where the rectum pierces the front wall of the same. Fig. 2 (*RE'*) shows the mouth of this duct at the left lower corner of the pericardium, and that of the right canal (*RE*) at the opposite corner. The former takes an oblique course along the side and floor of the papillary sac (*LK*), into which it opens between the papillæ. Throughout practically its entire extent it is lined with epithelial cells of moderate height apparently totally devoid of cilia.

The right renopericardial canal (*RE*) is a more slender duct, extending towards the gonoduct (*GO*) from the inner, forward angle of the pericardium. Its inner opening is relatively narrow and is situated immediately beneath the right branchial sinus (fig. 2, *S*). At the right of the pallial sinus (a branch of the branchial sinus) it may be seen entering the side of the gonoduct (fig. 3). In fig. 5, which is six sections farther forwards, the gonoduct may be seen opening freely into the cavity of the kidney at the point *GO*. In this connection it is to be noted that the ventral wall of the gonoduct is very thin and extends for some distance over the cavity of the kidney, unsupported by anything except the body wall above it. The right renopericardial canal in specimens of this size (1.5 cm.) discharges into the left side of the gonoduct, very close to the mouth of the latter—more so, in fact, than is shown at *GO* in fig. A.

An examination of large specimens of *Haliotis* by gross dissection did not at first appear to confirm the results given above. Accord-

[2] The sections shown in figs. 1, 2, 3, 4, 5 of Pl. XXX were made parallel with the line A–B of fig. A.

ingly similar sections were made through the same region in individuals of both species, and neglecting individual variation the series showed some interesting relations of organs decidedly unlike those just noted. From the study of specimens of smaller size it was found that between 1.5 and 3 cm. in length the renopericardial canal and gonoduct undergo a considerable amount of displacement. By referring to fig. 4, representing a section through an individual 3 cm. long, it will be seen that *the right renopericardial canal and gonoduct have their apertures facing each other.* Material of this size gave very satisfactory results with both species, and a study of sections of animals from 1.5–3 cm. long made it readily possible to trace where these organs go in assuming the adult condition.

In individuals 1.5 cm. long the renopericardial canal, which opens into the gonoduct near its end, gradually shifts forward to open by the latter by a common lipped mouth. From this stage on the common mouth of the canal and duct appears to change its position very little, if at all. At the same time the gonoduct, in some inexplicable way. forms for itself a second outlet into the kidney, a short distance away from the original mouth. It is this last named opening that is shown in fig. 4, and the one that in the adult serves for the discharge of the sex products.

The above statements are interesting not only in themselves, but they appear to me to explain certain other statements lately made. Tobler ('01) reported a second communication between the gonoduct and kidney in *Parmophorus*, and was followed by Totzaur ('02) with the statement that he had found a similar state of affairs in *Haliotis.* Neither of these investigators gives the point any explanation; nevertheless I believe both cases may come under the above interpretation.

Blood System.—In the following discussion of the organs of circulation an attempt has been made to explain certain apparently incorrect statements regarding this genus. Generally speaking the broader features of the system are already known. The work of Milne Edwards ('47), Lacaze Duthiers and especially Wegmann ('84) have done much to advance our knowledge along this line. Briefly reviewing their work in the light of the California species, it may be said that the heart is situated on the left posterior side of the visceral mass, a little behind the mantle cavity. The two auricles open into the ventricle, pierced by the rectum, and ventricular valves prevent the backward flow of blood. A small anterior aorta (fig. D, *Ao*) supplies blood to a portion of the mantle on the left side. The first part of its course is upon the dorsal wall of the rectum.

The lower posterior end of the ventricle originates the short common aorta, which at its first branch bears a membranous valve. The visceral aorta, arising posteriorly, bends beneath the posterior end of the visceral mass, supplying blood to the stomach, liver, gonad and that portion of the right kidney immediately behind the pericardium. The main artery continues anteriorly, coursing along in the wall of the body just above the epipodium. It soon develops the genital aorta, which proceeds towards the columellar muscle, giving off branches to the alimentary canal, right kidney, liver and gonad. It continues along the horn-

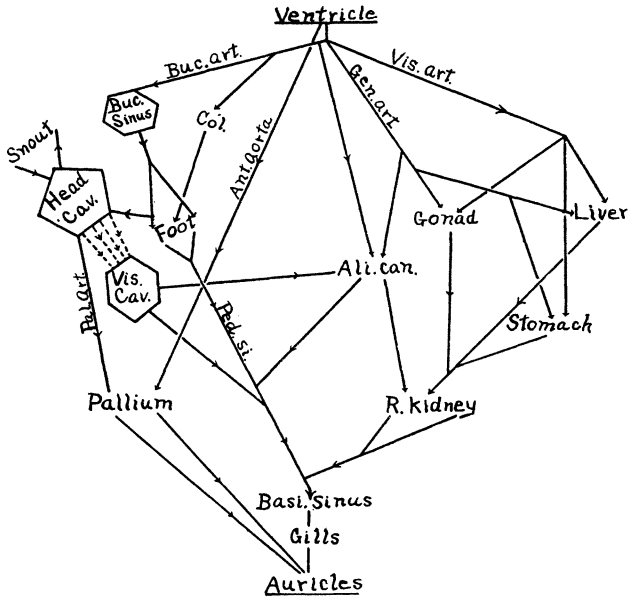

Fig. B.—Diagram of *Haliotis* circulation.

shaped portion of the visceral mass, branching freely through the liver and gonad.

The main or buccal aorta bends in a gentle curve to the buccal mass, developing, as it courses forward, branches to the viscera. The radula and its sheath lie freely in its lumen (figs. C, D, *BAo*), and more anteriorly it originates a branch of moderate size, which, owing to the fact that it supplies the great adductor muscle, may be known as the columellar artery (fig. D, *Co*). Reaching the head, the buccal aorta increases in calibre to envelop the buccal mass, thus forming the buccal sinus. Ventrally this sinus passes into the junction of the two pedal

arteries (fig. D, *Lpa*), with which, by three short canals, the sinus about the pleuro-pedal ganglia is brought into connection. The foot is thus supplied by the above-mentioned vessels and by the neural arteries surrounding the ventral nerve cords. The fact that so important a portion of the nervous system literally floats in a blood sinus gives an excellent clue to this portion of the system in *Haliotis*. By referring to fig. C it will be seen that the blood, having once gained the sinus about the pleuro-pedal ganglia, is free to work its way about the intestines, and to some extent the remainder of the viscera. The path is not so unobstructed as one might imagine from the figure, but even though a considerable amount of connective tissue does surround the gut, it is nevertheless penetrated by numerous fairly well defined channels.

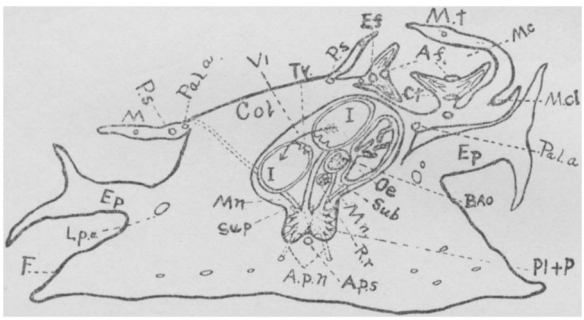

Fig. C.—Section passing through front end of columellar muscle and pleuro-pedal ganglia. *Aps*, anterior pedal sinus; *Apn*, nerves to front end of foot; *Lpa*, lateral pedal artery; *Mn*, mantle nerves; *Œ*, œsophagus; *Pal.a*, pallial artery; *Pl+p*, pleuro-pedal ganglia; *Ps*, pallial sinus; *Rr*, radula muscle; *Sub*, *Sup*, sub- and supra-intestinal nerve. For explanation of other letters see plate.

Following back along the cerebro-pleural and pedal connectives the blood finds its path readily into the head cavity. This surrounds the buccal cavity and lies between its wall and that of the head. In it the cerebral ganglia are situated, together with the salivary and sugar glands. It is somewhat indefinitely bounded, but it may be said that it extends posteriorly beyond the hinder border of the sugar glands. Its wall is of a spongy nature, permitting the blood to ooze out of the head cavity into the visceral cavity. The latter is a true hæmocele, as reported by Woodward for *Pleurotomaria*. At the left upper and posterior end of the head cavity there arises, by two or three roots, the main pallial artery. Passing along the left side of the neck in the body wall (fig. C, *Pal.a*), it turns somewhat to the left and enters the

extreme left edge of the mantle. Sending a branch anteriorly it bends sharply posteriorly and follows the mantle border around the visceral mass and up the right side. The sections show (figs. C, D, *Pal.a*) this vessel on both sides of the body. The artery becomes difficult to trace at the forward left side of the mantle which borders the columellar muscle. This is the vessel which Milne Edwards and Wegmann describe as a vein, but this is certainly an error, as it does not connect with the visceral cavity, but with that of the head.

The foot of *Haliotis* varies somewhat from that of the Old World species so far as the circulation is concerned. The single lateral pedal artery of each side of the epipodium in *H. rufescens* (figs. C, D, *Lpa*) is curiously enough represented in *H. tuberculata*, according to Wegmann, by two arteries, termed by him the superior pedal and inferior external pedal arteries. The foot is pierced freely by blood sinuses,

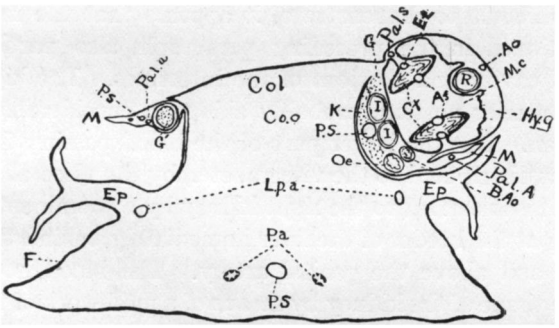

Fig. D.—Transverse section through middle of columellar muscle of *H. rufescens*. *Ao*, anterior aorta; *Co*, columellar muscle; *G*, *G*^{1}, gonad; *K*, anterior portion of right kidney. For other letters see explanation of plate.

and injections pass with ease throughout its entire extent even from arteries into veins or *vice versa*. It is therefore readily seen that the blood of the foot is collected into a large median sinus, of which two sections may be seen in fig. D, *PS*. At the front end of the foot this makes a gentle bend upward immediately behind the pleuro-pedal ganglia, and turning to the left along that side of the columellar muscle proceeds posteriorly. Throughout the remainder of its course, this sinus is partially imbedded in the anterior lobe of the right kidney (fig. D, *PS*), which it drains while *en route* to the basi-branchial sinus. Its lumen is of more than average size and may be readily followed. It is therefore with questioning that one considers Wegmann's statement to the effect that anteriorly this sinus in *H. tuberculata* empties into the visceral cavity. Can there be such a radical difference between two

species of the same genus? Here again it is interesting to note that *Pleurotomaria* and *Haliotis rufescens* agree, although Woodward, who had very little material, was not entirely sure of his ground.

The basi-branchial sinus (Pl. XXX, fig. 6, *Si*) is in reality but the branchial end of the median pedal sinus, that receives also a few veins (*NV*) from the right kidney. It is provided with a membranous valve (*V*), which, like the aortic valve, has not been hitherto described, so far as I am able to learn. The former suggests a like structure found in the Cephalopoda that likewise prevents a backward flow of blood from the ctenidia. Reaching these last-named organs through the afferent sinuses (*Af*, *Af'*) the blood is collected by the efferent vessels (figs. C, D, *Ef*), and with that of the pallial sinuses passes to the auricles, together with blood brought by several minor veins. Here, as in *H. tuberculata* and some other prosobranchs, there is a well-developed sinus connecting the two auricles.

Though difficult to demonstrate, it appears that the main venous sinus, mentioned in the preceding paragraph, also partially drains the visceral cavity and portions of the intestines. The kidney, especially the anterior portion, probably aids to a considerable extent in the operation. But the larger part of the blood passing through this organ is that distributed to the viscera, etc., by the visceral and genital arteries. This is carried to the right kidney by a prominent sinus that is seen lying at the border of the liver immediately behind the columellar muscle, and above the genital artery. The blood is distributed through the tissue of the kidney by means of a meshwork of fine vessels. In conclusion it may be said that the blood from the papillary sac drains into the basi-branchial sinus.

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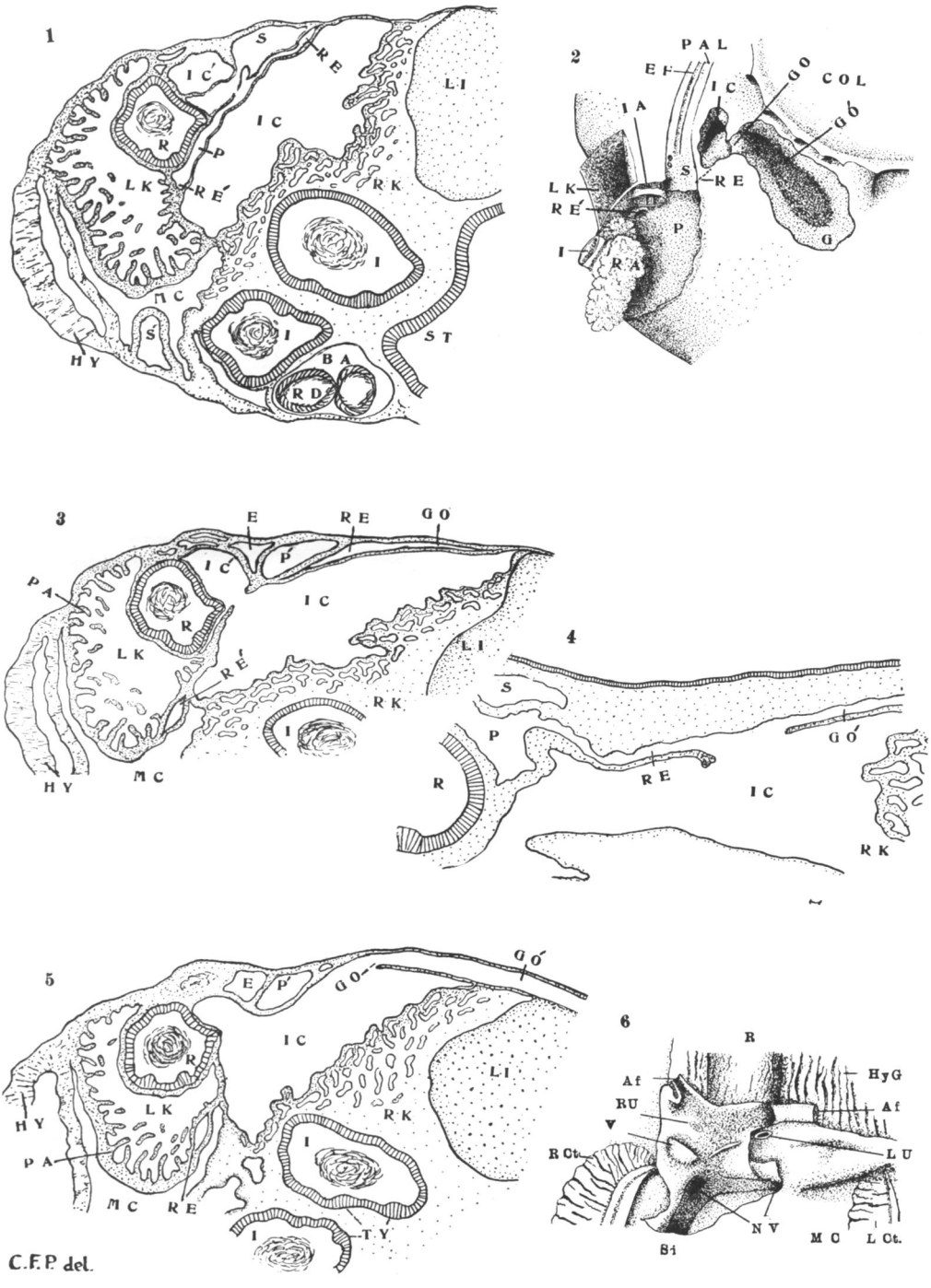
EXPLANATION OF FIGURES.

The following letters have been used in the explanation of the figures:

A, anterior aorta.
AO, main aorta.
BA, buccal aorta.
COL, columellar muscle.
EF, left efferent branchial sinus.
GA, genital aorta.
GO', gonoduct.
GO, gonoduct opening into right kidney.
I, intestine.
IA, blood sinus of left kidney.
IC', vestibule of right kidney.
LI, liver.
LU, left ureter.
PAL, right pallial sinus.
R, rectum.
RE, *RE'*, renopericardial canals.
RK, *RK'*, kidney lobes.
RU, right ureter.
VL, aortic valve.

EXPLANATION OF PLATE XXX.

Fig. 1.—Section through both kidneys of specimen of *Haliotis rufescens*, 1.5 cm. long, viewed posteriorly. *HY*, hypobranchial gland; *IC*, right kidney cavity; *RD*, end of radula; *ST*, stomach.
Fig. 2.—Portion of *H. rufescens* showing pericardium, left kidney, sinus and gonoduct. *COL*, columellar muscle; *G*, gonad.
Fig. 3.—Seventh section anterior to fig. 1. *E*, right efferent branchial sinus; *P'*, right pallial sinus.
Fig. 4.—Section through right renopericardial canal and gonoduct of *H. cracherodii*, 3 cm. long.
Fig. 5.—Sixth section anterior to that shown in fig. 3, showing opening of gonoduct into right kidney.
Fig. 6.—*H. rufescens*, dorsal wall of mantle reflected and basi-branchial sinus opened. *Af*, *Af'*, right and left afferent branchial sinuses; *HyG*, hypobranchial gland; *LCt*, left ctenidium; *LU*, left ureter; *MC*, mantle cavity; *NV*, veins from right kidney; *R*, rectum; *Si*, branchial sinus; *V*, valve.



PALMER ON HALIOTIDÆ